

Distribution and Abundance of Saltcedar and Russian Olive in the Western United States

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Over the past century, two introduced Eurasian trees, saltcedar (*Tamarix* spp.) and Russian olive (*Elaeagnus angustifolia*) have become wide spread on western United States of American (U.S.) rivers. This paper reviews the literature on the following five key areas related to their distribution and abundance in the western United States: (1) the history of introduction, planting, and spread of saltcedar and Russian olive; (2) their current distribution; (3) their current abundance; (4) factors controlling their current distribution and abundance; and (5) models that have been developed to predict their future distribution and abundance. Saltcedar and Russian olive are now the third and fourth most frequently occurring woody riparian plants and the second and fifth most abundant species (out of 42 native and non-native species) along rivers in the western United States. Currently there is not a precise estimate of the areas that these species occupy in the entire West. Climatic variables are important determinants of their distribution and abundance. For example, saltcedar is limited by its sensitivity to hard freezes, whereas Russian olive appears to have a chilling requirement for bud break and seed germination, and can presumably survive colder winter temperatures. Either species can be dominant, co-dominant or sub-dominant relative to native species on a given river system. A number of environmental factors such as water availability, soil salinity, degree of streamflow regulation, and fire frequency can influence the abundance of these species relative to native species. Numerous studies suggest that both species have spread on western rivers primarily through a replacement process, whereby stress-tolerant species have moved into expanded niches that are no longer suitable for mesic native pioneer species. Better maps of current distribution and rigorous monitoring of distributional changes though time can help to resolve differences in predictions of potential future spread. An adequate understanding does not yet exist of what fraction of western riparian zones is resistant to dominance by either of these species, what fraction is at risk and could benefit from intervention, and what fraction has been altered to the point that saltcedar or Russian olive are most likely to thrive.

Keywords area, extent, invasive species interactions, management, Russian olive, saltcedar, tamarisk

I. INTRODUCTION

Saltcedar (*Tamarix* spp.; also known as tamarisk) and Russian olive (*Elaeagnus angustifolia*) are introduced plants that are now frequent and abundant components of the woody riparian vegetation along many western United States of America (U.S.) rivers (Friedman *et al.*, 2005; Ringold *et al.*, 2008). Management strategies for dealing with these two species require knowledge of their distribution (extent of spread), their abundance in different ecosystems, and the ecological conditions that favor or hinder their spread or persistence. However, no recent reviews have been conducted to synthesize knowledge on their distribution and abundance. Earlier reviews tended to treat these plants as uniformly invasive, and remarks on their distribution emphasized the rapidity with which they spread, in keeping with the perception that they outcompeted and displaced native vegetation. For example, Di Tomaso (1998), reviewing the earlier literature, stated that saltcedar increased in area from 4,000 ha

in the 1920s (Neil, 1985) to 360,000 ha in 1965 (Robinson, 1965) and to 600,000 ha in 1987 (Brotherson and Field, 1987), representing a range expansion of 3–4% per year, at rates up to 20 km per river reach per year (Graf, 1978). Yet, none of the estimates were backed up with rigorous observational data. A more accurate, comprehensive, and up-to-date picture of the current distribution and abundance of these species is needed to inform strategies and tactics aimed at managing these species and associated riparian ecosystems.

Fortunately, there has been a great deal of ecological research conducted on saltcedar and to a lesser extent Russian olive over the past decade. These studies have produced a much more nuanced view of the invasive properties of these plants, and a more complete picture of their distribution and abundance in relation to native vegetation. This review draws on the recent literature to cover the following five key areas related to the distribution and abundance of these species in the western U.S. (Fig. 1): (1) the history of their introduction, planting, and spread; (2) their current distribution; (3) their current abundance; (4) factors that control their current distribution and abundance; and (5) models to predict their future distribution and abundance.

II. HISTORY OF INTRODUCTION, PLANTING, AND SPREAD

Saltcedar refers to a cluster of closely related species in the genus *Tamarix* (family Tamaricaceae) that were deliberately introduced to the United States in the nineteenth century from sources in southern Europe, Asia, and North Africa (Gaskin and Schaal, 2002; Gaskin and Kazmer, 2006). The species that are known to have been introduced and that have become naturalized are *T. ramosissima*, *T. chinensis*, hybrids between *T. ramosissima* and *T. chinensis*, *T. parviflora*, *T. gallica*, *T. canariensis*, and *T. aphylla* (also called athel, or athel pine). As early as the 1820s, saltcedar was advertised in U.S. horticultural catalogues, and by 1856 it was sold in California nurseries (Robinson, 1965). In the early 1900s, saltcedar was widely planted in the southwestern U.S. for windbreaks and protection from streambank erosion.

The majority of the invasive saltcedars in the western U.S. are *T. ramosissima*, *T. chinensis*, and hybrids between these (Gaskin and Schaal, 2002; Gaskin and Kazmer, 2006). In the 1930s, they escaped cultivation and spread rapidly along major western U.S. river systems (Robinson, 1965). They are now distributed widely in western U.S. riparian corridors (Friedman *et al.*, 2005; Ringold *et al.*, 2008), irrigation districts (Harrison and Matson, 2003; Cornell *et al.*, 2008), reservoir margins (Pearce and Smith, 2003, 2007), coastal salt marshes (Whitcraft *et al.*, 2007), and other habitats with moist soils or shallow groundwater. They are halophytes and, as such, are frequently found in saline habitats (Glenn and Nagler, 2005). The period of most rapid spread occurred during the 1940s to 1960s, coinciding with the era of major dam construction on western U.S.

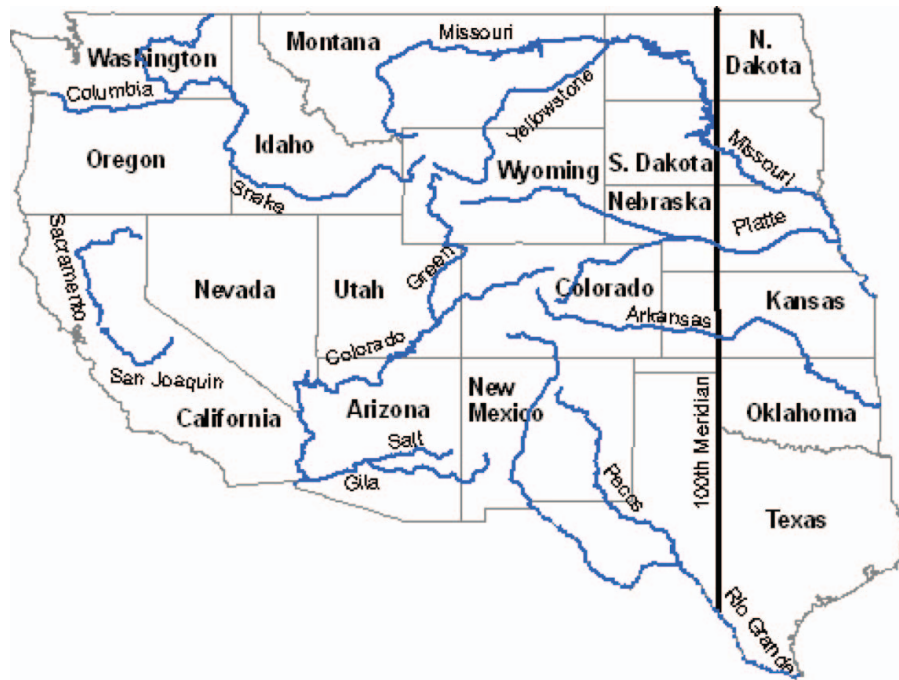


FIG. 1. Map of the western United States of America, with location of rivers and states included in the discussion in this article. State names are in bold type and river names follow the river course (color figure available online).

ivers, which created new habitats for saltcedar expansion along riverbanks and reservoir margins (Robinson, 1965).

The other *Tamarix* species are only locally abundant in North America. *T. gallica* and *T. canariensis* are most commonly distributed near the Gulf of Mexico coast in Texas, and there are some areas where *T. parviflora* has spread extensively, such as Cache Creek in California (Ge *et al.*, 2006). *T. aphylla* is a large tree that has been regarded as less invasive since it normally produces sterile seeds. However, it has been identified as an invasive species at Lake Mead National Recreation Area (Walker *et al.*, 2006). *T. aphylla* is locally abundant in various other places in the western U.S., particularly near where it was originally planted. In addition, *T. aphylla* has been found to hybridize with *T. ramossissima*, but there is no evidence that these hybrids have spread extensively (Gaskin and Shafroth, 2005).

Russian olive (*Elaeagnus angustifolia*, family Elaeagnaceae) is a small tree that was reportedly first brought to the U.S. in the 1800s by Russian Mennonites who planted it in hedgerows and for shade (Hansen, 1901). In the early 1900s, it was cultivated in several western states, and by the 1940s it was planted in windbreaks throughout the Great Plains (Read, 1958; Christensen, 1963; Tellman, 1997). Although it is listed as a noxious weed in many western states, Russian olive continues to be planted in windbreaks and horticultural settings, which was encouraged for years with state and Federal subsidies (Olson and Knopf, 1986; Haber, 1999). Russian olive escaped cultivation between the 1920s and 1950s (Christensen, 1963; Olson and Knopf, 1986), and it continues to spread (for example, Pearce and Smith,

2001; Lesica and Miles, 2001; Katz and Shafroth, 2003; Ringold *et al.*, 2008).

III. CURRENT DISTRIBUTION

There are no actual estimates of the number of hectares covered by these plants, as that would require detailed vegetation maps of the nation's riparian zones, a task that has not been undertaken. Although there is no current comprehensive inventory of these taxa in the United States, data that contain species presence (location)—and more rarely abundance—have been compiled on the National Institute of Invasive Species Science (NIISS) websites. Specific websites include <http://www.tamariskmap.org>, which focuses on saltcedar, and <http://www.niiss.org>, which provides information on various non-native species in the U.S. including Russian olive. In all, more than 20 disparate datasets have been compiled with coordinates for saltcedar, and more than 15 disparate datasets for Russian olive (Table 1). Most data are currently available at <http://www.niiss.org>. Data for Montana, Wyoming, and the southern Great Plains states were relatively sparse, and more data have been collected for saltcedar than for Russian olive.

Saltcedar is widely distributed along major river systems and reservoirs in Arizona, Utah, Colorado, Texas, New Mexico, southern California and Nevada, and western Oklahoma and Kansas (Figure 2a, 3a). Although not shown in Figure 2a, saltcedar also occurs in northern Mexico (Harrison and Matson, 2003; Cornell *et al.*, 2008; Scott *et al.*, 2009). Since the 1950s and 1960s, saltcedar has expanded its distribution

TABLE 1
Datasets found to include data for Russian olive and saltcedar

Data source	Russian olive sample size	Saltcedar sample size	On NIISS.org
Bay, 2008		79 points	No
Bradshaw, 2006		2931 points	Yes
Colorado Department of Transportation, 2002	55 polygons	48 polygons	Yes
Colorado project, www.niiss.org		53 points	Yes
Colorado State Parks mapping data (Unpublished, 2003)	124 points 84 polygons	18 points 5 polygons	Yes
Davern, 2006		639 points	Yes
Fingerprinting biodiversity (CSU and USGS field data), www.niiss.org	69 points	135 points	Yes
Friedman and others (2005) data	144 points		Yes
Sexton and others (2006) data		20 points	No
Grand Staircase Escalante National Monument (Evangelista and others 2008)	52 points	1881 points	Yes/ No
Hubbard Lake, www.niiss.org		10 polygons	Yes
Uowolo, 2005		11 points	No
National Park Service (2003) GIS data	3 points	1291 points	Yes/ No
National Wildlife Refuge Project	4 points	2 polygons	Yes
Nevada mapping data from NASA Ames (Sengupta and others, 2005)		154 points	Yes
NIISS Citizen Science Website Projects (www.citsci.org)	16 points	100 points	Yes
North Dakota Department of Agriculture, 2003		2648 points	Yes
Otero County, Colo. (Kelley, 2003)		1422 points	No
UC Davis plot data (Unpublished, 2007)	11 points		No
Robinson, 1965		143 points	Yes
Royal Gorge (Vieira, 2003)	14 points	19 points	No
South Dakota Department of Agriculture, 2006		16 polygons	Yes
Southwest Exotic Plant Mapping Program (Thomas and Guertin, 2007)	366 points	899 points	Yes
Tamarisk Coalition, 2008		2267 polygons	Yes
Colorado Natural Heritage Program, 2008		11 points	No
Utah BLM office, 2006	248 points	247 points	No
Northwest saltcedar data (Bridgett Naylor, personal communication)		1044 points	No

Note: Data from www.niiss.org were downloaded on July 2, 2008. Polygon sizes varied among studies.

in the northern Great Plains states (Pearce and Smith, 2007). Montana has significant populations of saltcedar in riparian and wetland areas, and especially along the margins of reservoirs with fluctuating water levels (Sexton *et al.*, 2006). In North and South Dakota, saltcedar is listed as a noxious weed (National Resources Conservation Council, 2008), although, in comparison to Montana, it appears to be relatively scarce in South Dakota as well as Nebraska and Wyoming. However, this may be an artifact of differences in sampling intensity.

Friedman *et al.* (2005) concluded that saltcedar, which produces numerous easily dispersed seeds after only one year of growth, has spread widely across the western U.S. and probably already occupies most of the locations to which it is suited, al-

though further northward expansion could occur due to climate warming, evolution of frost tolerance, or reservoir construction. A comparison of the relatively recent map in Friedman *et al.* (2005) with the much older one in Robinson (1965) suggests that the range of saltcedar has not expanded much in four decades. Ringold *et al.* (2008) estimated saltcedar to be present on 20.9% of the assessed stream lengths in their "xeric" climate region (southern California, Nevada, Arizona, western New Mexico, Southern Utah, and Southwestern Colorado), and on 7.7% of the assessed stream length in their "plains" climate region (North and South Dakota, and the plains of eastern Montana, Wyoming, and Colorado).

Russian olive is now found in all but the southeastern states and occurs across the southern tier of Canadian provinces

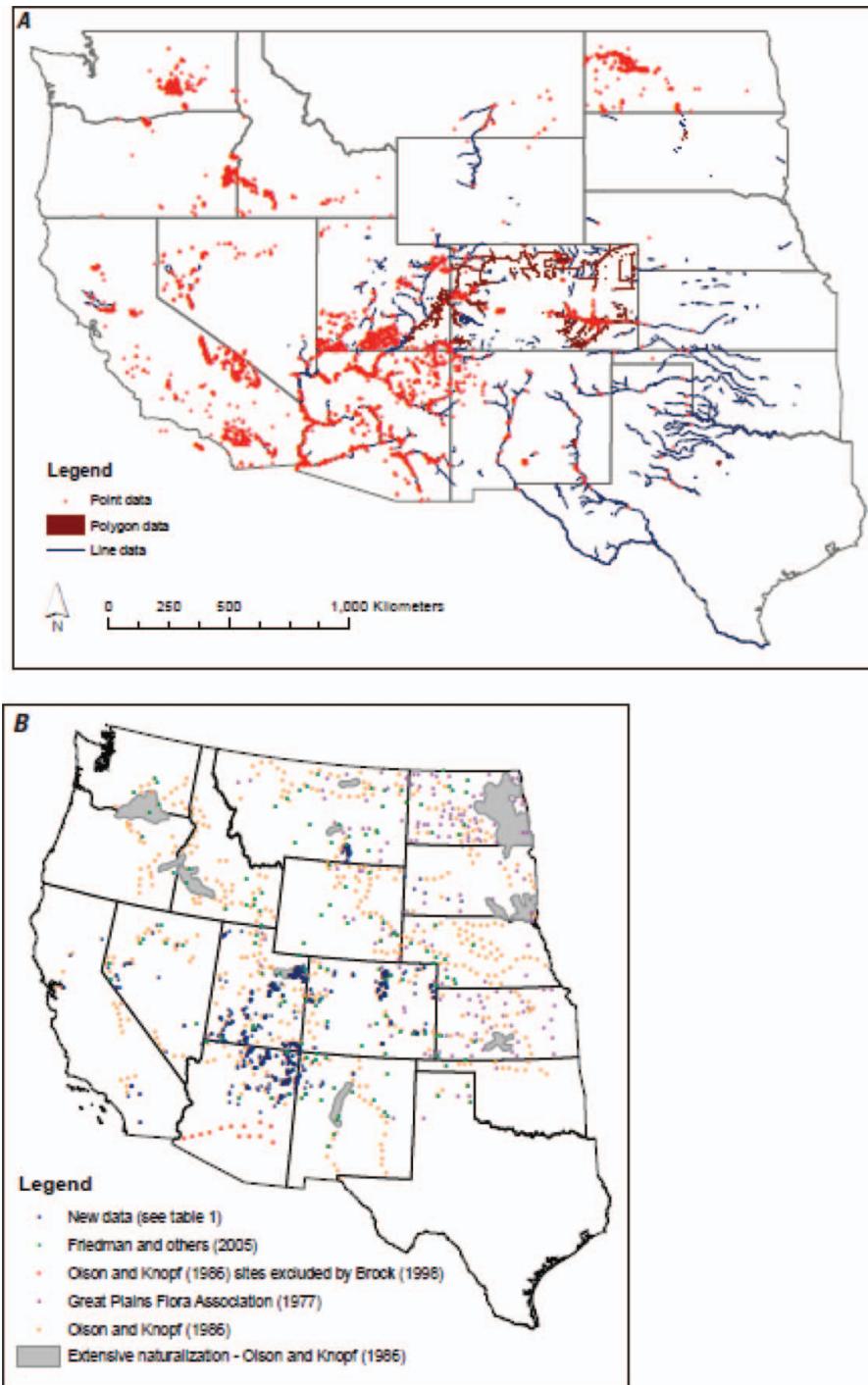


FIG. 2. Recorded locations of (a) saltcedar from compiled datasets listed in table 1, displayed as point, line, or polygon features, reflecting the format in which they were collected; and (b) Russian olive from compiled datasets in table 1 (used in modeling) merged with the distribution of Russian olive in 17 western states from Katz and Shafroth (2003). Colors represent reports of occurrence based on different studies cited in Katz and Shafroth (2003) (color figure available online).

(<http://www.plants.usda.gov/java/profile?symbol=ELAN>), although it is not naturalized in all of these locations. Collectively, various publications (cited in Katz and Shafroth, 2003) indicate that it has become naturalized along most of the major river sys-

tems in the Great Plains, and in mid-elevation rivers in all the southwestern states (Figs. 2b, 3b). It is found along many of the major western river systems, including the Platte, Middle Rio Grande, Snake, Yellowstone, Upper Missouri and its tributaries,

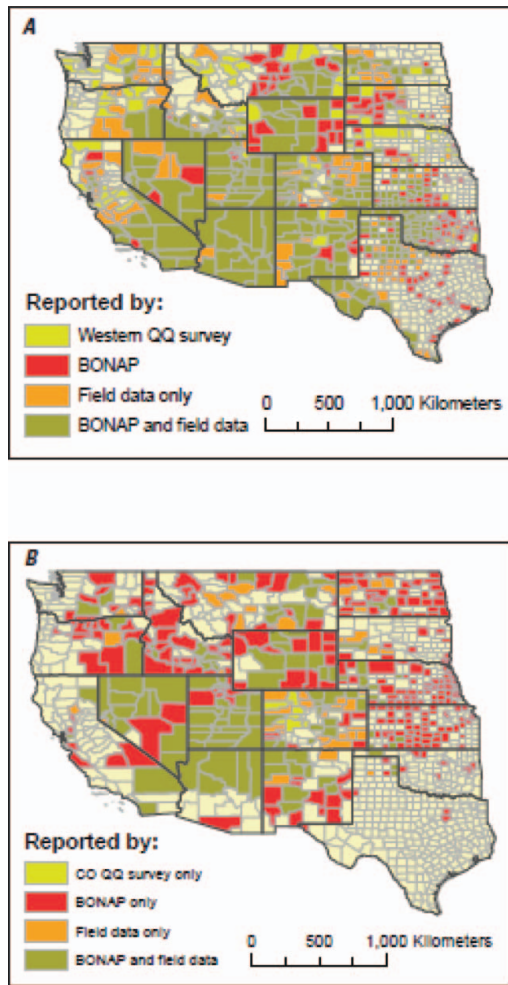


FIG. 3. County distribution of (a) saltcedar and (b) Russian olive, including counties identified in the Biota of North America Program dataset, counties with field data from Figure 1, and counties with quarter quadrangle acreage greater than zero in the western U.S. (saltcedar) and in Colorado (Russian olive). Differences in county information (all but the dark olive-colored counties) indicate there are still data gaps in the various data sets available for the two species (color figure available online).

and the Upper Colorado River and its tributaries. Ringold *et al.* (2008) found that Russian olive occurred on 17.2% of stream length in their xeric region and 19.9% of stream length in their plains region. Russian olive has relatively large seeds that are not dispersed as rapidly as those of saltcedar (Katz and Shafroth, 2003); thus, it is possible that its seeds have not yet reached all of the suitable areas in western North America (Friedman *et al.*, 2005).

IV. CURRENT ABUNDANCE

Mere presence is not an indication that saltcedar and Russian olive are problematic; relative abundance is more important for determining whether these species actually have undesirable effects (for example, van Riper *et al.*, 2008). However, relative abundance data currently available for these species are less

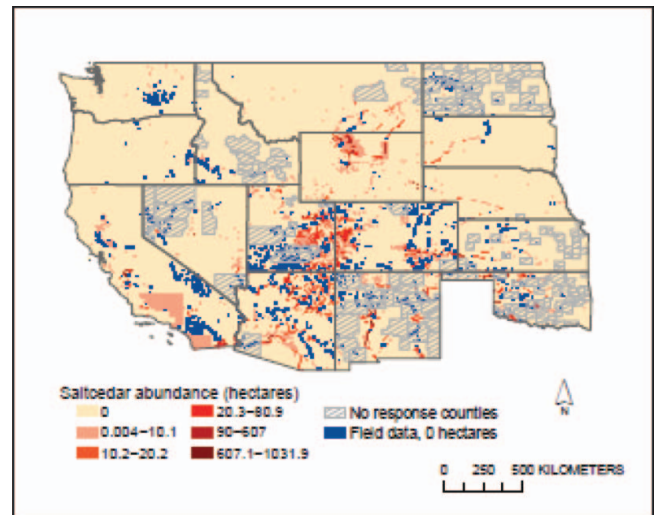


FIG. 4. Quarter quadrangle estimates of saltcedar acreage surveyed at the county level in 2004. Quarter quadrangles from where field data reported saltcedar but where the acreage estimates were zero are highlighted in blue. Dataset produced by the Western Weed Coordinating Committee with funding from the Center for Invasive Plant Management (color figure available online).

comprehensive than presence/absence data. Furthermore, the abundance metrics measured and details studied have varied across scales and studies.

At regional or landscape scales, the Western Weed Coordinating Committee asked county weed coordinators to estimate saltcedar acreage for each quarter quadrangle (ca. 40 km²) in their jurisdiction and based their report on those figures (Fig. 4). The data reported, however, were based on expert knowledge rather than actual field data; thus, the geographic coverage tends to be incomplete and inconsistent, creating large data gaps. Field data are also suspected of being incomplete. For example, data collected by the National Institute of Invasive Species Science revealed saltcedar presence in 1,899 of the quarter quadrangles that were classified previously as having zero acres of saltcedar or where the county weed coordinator did not respond to the survey, and more than half of those quadrangles were located in counties that reported zero acres in the survey. The results in Figure 4, therefore, should be interpreted cautiously, even though they provide the only estimates based on consistent methods for abundance across the entire western United States.

Another issue with available saltcedar abundance data is that the number of acres it occupies typically has been estimated at different times using different methods, and only rarely have areas where the species is merely present been differentiated from areas where it is dominant. Robinson (1965) compiled information from various sources to arrive at an estimate of 360,000 ha across the western U.S. in 1961. This figure has been referenced repeatedly, sometimes slightly modified, for over 40 years without rigorous updating. Thus, currently there is no credible estimate of the abundance of saltcedar in the western

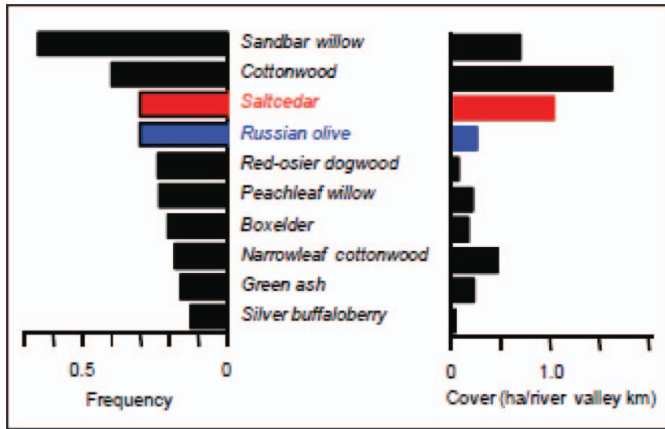


FIG. 5. Frequency of occurrence and normalized vegetation cover of *T. ramossissima* and *E. angustifolia* compared to native trees on western U.S. rivers, from a survey of woody riparian vegetation at 475 randomly chosen stream gauging stations reported in Friedman and others (2005). Modified from Figure 1 in Friedman *et al.*, 2005 (color figure available online).

United States. It may be reasonable to assume that there are at least 360,000 ha within which it has a history of occurring.

Friedman *et al.* (2005) measured canopy cover of both saltcedar and Russian olive, plus 42 other woody plant species along river reaches adjacent to 475 randomly chosen gauging stations, in the 17 contiguous states west of the 100th meridian. Saltcedar and Russian olive were the third and fourth most frequently occurring woody riparian plants and the second and fifth most abundant (based on canopy cover; including native species; Figure 5). Saltcedar was dominant in low-elevation, southwestern riparian corridors, but only occasionally was it dominant above the 41st parallel (as along reservoir margins in Montana). In contrast, Russian olive was most abundant in the northern Great Plains (Figure 6).

Although saltcedar and Russian olive were introduced to the U.S. over 100 years ago and are widely naturalized and present in many river systems and other suitable habitats, Stromberg *et al.* (2007b) and Merritt and Poff (2010) found that they are rare or subdominant on some rivers, co-dominant with native trees on others, and dominant on still others. Examples of rivers that support dense, nearly monotypic stands of saltcedar include the Lower Colorado from Lake Mead (on the Nevada/Arizona border) to the U.S.-Mexico border (Nagler *et al.*, 2007), the Rio Grande below Elephant Butte Reservoir in southern New Mexico (Hudgeons *et al.*, 2007), and the Pecos River in New Mexico and Texas (Hart *et al.*, 2005) (Figure 4). Floodplains vegetated with mixtures of saltcedar and native trees represent the most common current condition along western river segments, including the following: Middle Rio Grande (Dahm *et al.*, 2002; Akasheh *et al.*, 2008; Walker *et al.*, 2008); the Lower San Pedro (Brand *et al.*, 2008); the San Juan River below Navajo Dam in Colorado, New Mexico, and Utah (authors' observations); the Colorado River below Glen Canyon Dam in Grand Canyon (Groeneveld and Watson, 2008; Mortenson *et al.*, 2008); the Bill Williams River below Alamo Dam in Arizona (Shafroth *et al.*, 2002); the Salt River above Roosevelt Lake and the Agua Fria River in Arizona (Stromberg *et al.*, 2007b; Boudell and Stromberg, 2008); the Arkansas River in Colorado (Nelson and Wydoski, 2008); and the delta of the Colorado River in Mexico (Nagler *et al.*, 2005).

As with saltcedar, Russian olive abundance varies considerably among different rivers and different reaches within a given river system (Table 2). On parts of the Snake River in Idaho, Russian olive can grow in dense stands constituting 80% of the vegetation cover. On the Middle Rio Grande, Marias, and Yellowstone Rivers, it can grow as an understory plant in cottonwood stands or as a co-dominant plant with cottonwood (Lesica and Miles, 2001; Dahm *et al.*, 2002).

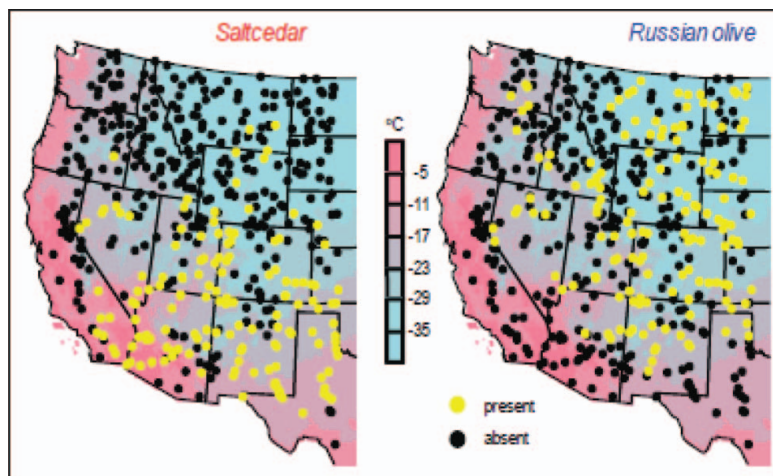


FIG. 6. Presence and absence of saltcedar and Russian olive at 475 sample locations in the western U.S. and associated mean annual minimum temperature. Modified from Figure 2 in Friedman *et al.*, 2005 (color figure available online).

TABLE 2

Density and percent canopy cover of Russian olive trees on western U.S. rivers

River or Location	Density (Plants/ha)	Cover (%)
Rio Grande, N.M.	0–566	0–43.3
Chinle Wash, Ariz.	430–1150	25–78
Duchesne R., Utah	NA	50
Milliken, Colo.	NA	40
Arikaree R., Colo.	0.7–225.3	N/A
Republican R., Colo.	4.3–314.3	NA
Platte R., Nebr.	NA	2.2–24.5
Marias R., Mont.	20–760	NA
Yellowstone R., Mont.	20–5120	NA
Snake R., Idaho	0–940	0–81.2

Note: Table is modified from Katz and Shafroth (2003), which also cites the original published sources.

V. FACTORS THAT CONTROL CURRENT DISTRIBUTION AND ABUNDANCE

A. Continental and Landscape-Scale Factors

Figures 2 and 6 illustrate the tendency for saltcedar to have a more southerly distribution than Russian olive. Friedman *et al.* (2005) expressed this quantitatively as a function of mean annual minimum temperature (Figure 7). Saltcedar is limited by its sensitivity to hard freezes, whereas Russian olive appears to have a chilling requirement for bud break and seed germination, and presumably it can survive colder winter temperatures. However, populations of saltcedar certainly occur in the northern Great Plains states (for example, Pearce and Smith, 2003; Sexton *et al.*, 2006; Figures 2a, 3a, 6). Friedman *et al.* (2008) found that there was inherited variation in cold hardiness in North American *Tamarix*, which, combined with hybridization and climate warming, could permit range expansion northward. Although both saltcedar and Russian olive occur east of the Mississippi River, generally they are not regarded as pest species in these states.

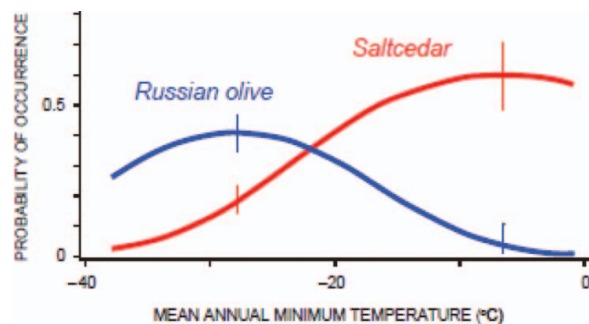


FIG. 7. Probability of occurrence of saltcedar and Russian olive as a function of mean annual minimum temperature. Modified from Figure 3 in Friedman *et al.*, 2005 (color figure available online).

At the landscape scale, water availability is the clearest factor controlling distribution of these taxa in the arid and semiarid western United States (Jarnevich and Reynolds, 2010). Both species appear to require supplemental moisture relative to that available in upland environments, which explains their distribution within river floodplains, along reservoir margins, and near other sources of supplemental moisture such as springs or irrigation canals. There have been reports that saltcedar and Russian olive are able to occupy “uplands” (Knopf and Olson, 1984; Morisette *et al.*, 2006); however, we have found no literature indicating that saltcedar has colonized upland areas surrounding riparian corridors. Rather, it appears that the term “upland” has been used by some to denote terraces or small drainages within an upland matrix that, though drier than more mesic floodplain surfaces, are still part of the bottomland or at least are areas with a moisture supplement. Saltcedar and Russian olive are relatively drought tolerant and therefore may be able to occupy some areas within the bottomland, such as terraces, which are typically unsuitable for native, mesic riparian trees and shrubs (for example, cottonwoods and willows). Along Chinle Creek, Arizona, Russian olive seedlings became established on terraces where precipitation is the only water source, and plants up to 15 years old survived on only soil water (Reynolds and Cooper, 2010). Within a bottomland setting, Russian olive can establish within and occupy some sites that saltcedar typically does not, such as wet meadows and cottonwood understory (for example, Currier, 1982; Lesica and Miles, 2001; Katz and Shafroth, 2003).

B. River Reach and Site-Scale Factors

As described above, the presence of saltcedar and Russian olive varies considerably between sites and river reaches across the western United States. In this section, we discuss the environmental conditions under which these species remain subdominant or rare and the conditions under which they thrive and become of concern to resource managers. We discuss the following five factors that have been shown to be major drivers of the distribution and abundance of riparian vegetation in the western U.S. at river-reach and site scales: (1) high flows and fluvial disturbance regimes; (2) low flows, alluvial groundwater conditions, and water availability; (3) soil texture; (4) soil and aquifer salinity; and (5) fire regimes. We show how streamflow regimes and associated processes drive or influence these five key factors from the standpoint of three river categories that vary in their levels of streamflow regulation and other anthropogenic perturbations.

1. High Flows and Fluvial Disturbance Regimes

Arguably the most important site factors that determine the suitability for different riparian plants are those associated with the hydrologic regime, including high flows (and associated disturbance), low flows, and alluvial groundwater dynamics

(Stromberg *et al.*, 2007a). Various aspects of a river's flood regime (including frequency, magnitude, duration, timing, and rate of change; see Poff *et al.*, 1997) can influence riparian vegetation dynamics. Natural flood regimes and associated fluvial processes are the main drivers of structural and compositional diversity of riparian vegetation (Hughes, 1997). In the western U.S., aspects of flow regimes that may favor native pioneer trees (cottonwoods and willows, genera *Populus* and *Salix*) over *Tamarix* and *Elaeagnus* or allow a mix of native species and *Tamarix* and *Elaeagnus* include the following: (1) floods that are large enough to create bare, moist germination sites; (2) flood timing that is synchronized with the seed dispersal period of native pioneer trees; (3) flood recession that is slower than seedling root growth; (4) base flows that provide continued high water availability; and (5) a lack of subsequent floods until plants are large enough to resist flood-induced physical damage (Mahoney and Rood, 1998; Hughes *et al.*, 2001). Also, the frequency of suitable recruitment flows strongly influences the heterogeneity and age-class diversity of riparian forests in western North America (Mahoney and Rood, 1998). Russian olive is less flood- and disturbance-dependent than cottonwood, willow, or saltcedar, and it is more shade-tolerant (Shafroth *et al.*, 1995; Lesica and Miles, 1999; Katz *et al.*, 2001; Katz and Shafroth, 2003; Katz *et al.*, 2005; Reynolds and Cooper, 2010). Although not addressed here, non-hydrologic disturbance factors such as grazing also can affect the spread of non-native plant species (Lozon and MacIsaac, 1997).

2. Low Flows, Alluvial Groundwater, and Associated Water Availability

Low flows and alluvial groundwater dynamics strongly influence which riparian taxa occupy particular sites (Stromberg *et al.*, 2007a). Different plant species and communities are associated with particular ranges of depth to groundwater (Meinzer, 1927; Stromberg *et al.*, 1996), though groundwater regimes often are characterized by significant intra- and inter-annual variation (Scott *et al.*, 1999, 2000; Shafroth *et al.*, 2000). Cleverly *et al.* (1997) showed that over time, saltcedar can become dominant on drought-affected rivers. Lite and Stromberg (2005) developed a model for the San Pedro River in Arizona that determines whether sites will be dominated by stands of non-native saltcedar or native cottonwoods and willows based on thresholds in water availability. The native trees dominated sites where surface flow was present more than 76% of the time, interannual fluctuations in the alluvial groundwater table were less than 0.5 m, and the average maximum depth to the water table was less than 2.6 m, based on two years of data collection. Specific reports of Russian olive tolerance to particular groundwater or low-flow conditions are lacking; however, Russian olive appears to be able to tolerate a broad range of soil moisture conditions within river bottomlands (Campbell and Dick-Peddie, 1964; Lesica and Miles, 2001; Katz and Shafroth, 2003; Reynolds and Cooper, 2010).

3. Soil Texture

Soil texture can affect soil moisture, salinity, nutrient availability, aeration, height of the capillary fringe above the water table, and competitive interactions between saltcedar, Russian olive and native species (Sher and Marshall, 2003). For example, fine-textured soils are associated with a more extensive capillary fringe as well as higher water- and nutrient-holding capacities compared to coarse-textured soils. Salinity may be higher in clay soils because of the higher cation exchange capacity. Saltcedar grows on a wide range of bottomland sediments, including variable surface and subsurface textures, ranging from fine sands to dense clays. The range of soil types that support Russian olive has not yet been defined.

4. Salinity of Soils and Aquifers

Plants vary in their tolerance of soil salinity; thus, elevated levels of soil salinity can greatly influence the relative abundances of saltcedar, Russian olive, and native taxa (Shafroth *et al.*, 2008). All western rivers carry some dissolved salts, and some, such as the Lower Colorado (0.8 g/l; Nagler *et al.*, 2009) and the Pecos (4–10 g/l; Hart *et al.*, 2005), have relatively high salinities. Salts enter rivers as leachate from natural marine deposits and other sources and can concentrate as rivers are used for irrigation. Salinity of floodplain soils can become concentrated due to lack of flushing from overbank flows (Jolly *et al.*, 1993). As a result, soil salinity on many surfaces has increased to levels that no longer support non-halophytic riparian plants.

Saltcedar is a halophyte, with 50% growth reduction at a salinity level of 35 g/l (equal to seawater salinity; Glenn *et al.*, 1998). On the other hand, cottonwood and willows are glycophytes, with 50% growth reduction occurring at only 5 g/l salinity. In addition to influencing the survival and growth of established plants, high levels of soil salinity can reduce seed germination and seedling establishment (Shafroth *et al.*, 1995). Russian olive is more salt tolerant than the native trees it grows with, but not as tolerant as saltcedar (Monk and Wiebe, 1961; Carman and Brotherson, 1982; Kefu and Harris, 1992). In particular, Russian olive has high tolerance of alkaline conditions (Stoeckeler, 1946; Read, 1958; Katz and Shafroth, 2003).

5. Fire Regimes

Another factor that appears to favor saltcedar dominance over native taxa is fire, though evidence for this is mixed in the few reports on the topic (Busch, 1995; Busch and Smith, 1995; Ellis, 2001). Wildfires in riparian systems of the southwestern U.S. have increased in recent decades, largely as a result of dense buildup of combustible litter and an increase in anthropogenic ignitions (Busch, 1995; Busch and Smith, 1995; Ellis, 2001). Flow regulation indirectly promotes fire in riparian ecosystems because, without floods that transport and export this material and promote its decomposition, potentially combustible plant litter accumulates (Ellis *et al.*, 1998). Saltcedar resprouts readily after fires, which can reinforce its dominance over time

(Busch, 1995; Busch and Smith, 1995). On the Lower Colorado River and its tributaries, the abundance of saltcedar and the native shrub arrowweed (*Pluchea sericea*) tends to increase following fire, whereas abundance of cottonwood, willow, and mesquite (*Prosopis* spp.) tends to decrease (Busch, 1995; Busch and Smith, 1995). However, in a study along the Middle Rio Grande, resprouting of native cottonwood and willow following fire equaled or exceeded that of saltcedar (Ellis, 2001).

C. Relationships between Abundance of Saltcedar and Russian Olive and Degree of Flow Regulation

Two recent studies (Stromberg *et al.*, 2007b; Merritt and Poff, 2010) examined the abundance of saltcedar relative to native pioneer trees in the context of flow regulation across multiple rivers in the western United States. Stromberg *et al.* (2007b) compared saltcedar to cottonwood and willow abundance on 24 river reaches in the Gila and Lower Colorado drainage basins of Arizona. The authors presented the following two main comparisons of abundance levels: (1) between reaches with perennial and intermittent surface flow, and (2) within the perennial reaches, between free-flowing and flow-regulated reaches. Streamflow conditions were strong determinants of vegetation structure. Cottonwood and willow were dominant on perennial reaches that still had a natural flow regime; saltcedar made up less than 10% of the vegetation cover on these streams. In contrast, saltcedar was abundant on reaches with intermittent flow (either naturally or due to water extraction for human uses) and on flow-regulated reaches. Merritt and Poff (2010) related the probability of successful recruitment and the relative dominance of cottonwood and saltcedar to the degree of flow alteration at 64 sites along 13 perennial rivers across arid and semi-arid western United States. The authors found that although saltcedar recruitment was highest along unregulated river reaches, it remained relatively high across all levels of flow regulation. Cottonwood recruitment, on the other hand, was severely limited by even low levels of flow alteration. Similarly, saltcedar attained relative dominance over cottonwood along reaches with moderate to high levels of flow alteration.

These studies reinforce a large number of other studies that elucidate the mechanisms of vegetation change on western rivers. Under natural or naturalized flow regimes, cottonwood and willow seedlings often co-occur with and may outcompete those of saltcedar (Stromberg, 1997; Sher *et al.*, 2002; Nagler *et al.*, 2005; Bhattacharjee *et al.*, 2009; Reynolds and Cooper, 2010). In some parts of the western United States, seeds of native species germinate earlier in the year than saltcedar and tend to grow faster during the first year (Shafroth *et al.*, 1998). Cottonwood and willow trees can grow taller than saltcedar, eventually overtopping them. Saltcedar shrubs prefer full sun and do not grow well as understory or midstory plants. In their natural state, many western U.S. rivers had periods of high flow in winter/spring or summer due to winter rains or snowmelt that caused overbank flooding. These flows washed salts from the soil, created sites favorable for seed germination, and recharged alluvial

aquifers away from the river. Especially high flows reworked the river bed, cut new channels, and scoured out undergrowth to provide new areas for trees to establish. These patterns and processes are evident in upper reaches of the major rivers in Sonora, Mexico where native trees are dominant and saltcedar is a minor component of the flora (Scott *et al.*, 2009).

By contrast, on highly flow-regulated perennial rivers with dams, extensive water diversions, and channelization, conditions may favor saltcedar (Stromberg *et al.*, 2007a, b; Merritt and Poff, 2010). These rivers rarely have any overbank flooding and the important associated fluvial disturbance and salt-flushing described above. As a result, native trees can no longer establish on the floodplains; over time, these surfaces may become dominated by saltcedar as native trees die due to old age or disease.

As mentioned above, salinity plays a key role in the replacement of native trees by saltcedar on regulated rivers. Saline return flows from irrigation districts along many rivers enter as subsurface flows or surface drainage, concentrating salinity. Soil and alluvial aquifer salinity have become elevated in the bottomlands of many arid-region rivers where flow regulation has reduced or eliminated overbank flooding and associated leaching or flushing of salts (Jolly *et al.*, 1993; Anderson, 1998). As a result, soil salinity on many surfaces has increased to levels that saltcedar can tolerate but many native riparian taxa (such as cottonwood and willow) cannot.

In addition to salinity constraints, flow-regulated rivers often have deeper alluvial water tables due to diversion of water away from the river and groundwater pumping. Numerous studies have shown that saltcedar is drought tolerant and can access aquifers as deep as 10 m (Horton *et al.*, 2001), whereas native trees require shallow aquifers (2–3 m), which no longer exist along many flow-regulated rivers (reviewed in Glenn and Nagler, 2005).

Many western U.S. rivers are intermediate between free-flowing and completely flow-regulated. The Middle Rio Grande in New Mexico is an example (Dahm *et al.*, 2002; Akasheh *et al.*, 2008; Walker *et al.*, 2008). Flow in this segment is dammed and diverted for irrigation and municipal use. However, there is still perennial flow in the river and an annual pulse-flow regime augmented by occasional large releases that produce overbank flooding. The Middle Rio Grande supports a mixed riparian forest in which cottonwood and saltcedar are co-dominants, and Russian olive is present as a mid-story species under the native trees. Establishment of new cottonwood stands, however, is uncommon. As mentioned in the “Current Abundance” section (above), floodplains with mixed stands of saltcedar and native trees seem to be the most common. This likely reflects the greater number of rivers with intermediate levels of flow regulation.

Although there are many fewer studies focused on Russian olive than saltcedar, Russian olive distribution and abundance are also apparently associated with flow regulation (Ringold *et al.*, 2008). As discussed above, because Russian olive can

germinate, establish, and grow in the presence of competition from understory vegetation and/or canopy cover, it does not require bare fluvial surfaces that are commonly created by flood-related processes (e.g., Scott *et al.*, 1996). Flow regulation typically reduces the rate and extent of creation of new, bare fluvial surfaces, and thus could provide more suitable sites for the more shade-tolerant Russian olive than for species such as cottonwood and willow that depend on these bare sites (Shafroth *et al.*, 1995; Reynolds and Cooper, 2010). The tendency for Russian olive to have expanded on regulated river reaches has been reported in several specific cases (Akashi, 1988; Lesica and Miles, 1999, 2001; Katz *et al.*, 2005), and was also observed in a recent regional study of western rivers (Ringold *et al.*, 2008). Russian-olive is also able to persist on sites high above the water table (Reynolds and Cooper, 2010).

VI. MODELS TO PREDICT FUTURE DISTRIBUTION AND ABUNDANCE

Habitat suitability models can fill data gaps in survey records and potentially predict areas where future spread is more or less likely. The models can highlight priority locations for future surveying and monitoring and inform decision makers and land managers as to which areas are not currently occupied by non-native species. Here, we critically review modeling efforts.

Existing models for saltcedar include one developed by Evangelista *et al.* (2008), who modeled saltcedar distribution for Grand Staircase-Escalante National Monument by using distance to water, slope, solar radiation, soil wetness, and aspect as explanatory variables for presence or absence of saltcedar. The authors divided a set of presence-absence databases into training sets and validation sets, and found they could reasonably predict where saltcedar should occur. However, they did not address abundance questions.

Morisette *et al.* (2006) used remote sensing and presence-absence data to create a habitat suitability map for saltcedar. For Arizona, Utah, Colorado, New Mexico, Texas, Nevada, and California they estimated that 8–30% of the states' map pixels, totaling 35 million ha, contained "highly suitable" habitat for saltcedar. About twice that amount of land was rated as moderately suitable. They concluded that saltcedar has great potential for further spread in these states. However, caution is needed in accepting this conclusion, because the area containing highly suitable habitat would be limited to areas such as river floodplains and reservoir margins, and thus likely would be a very small fraction of the total pixel area.

Friedman *et al.* (2005) modeled the distribution of saltcedar and Russian olive at the scale of the western United States as a function of mean annual minimum temperature (Figure 7). Their results, based on Gaussian logistic regression, indicated that the probability of saltcedar occurrence declined with decreasing mean annual minimum temperatures, whereas the probability of Russian olive occurrence increased with lower mean annual minimum temperatures.

Jarnevich *et al.* (2011) and Jarnevich and Reynolds (2010) recently developed new habitat suitability maps for both saltcedar and Russian olive using most of the field data locations described above (Figure 8a and b), an expanded suite of predictor variables, and the Maximum Entropy (Maxent) modeling technique (Phillips *et al.*, 2006). Predictor variables included bioclimatic variables, topographic variables, and others such as distance to water. Distance to water was based on the National Atlas of the United States hydrography layer, and is the shortest distance from one pixel to another pixel containing a water body in the layer used. Maxent provides a metric to evaluate model performance (hereafter, "evaluation value"), with values ranging between 0.5 and 1.0. An evaluation value of 0.5 indicates no discrimination ability; values between 0.7 and 0.8 are acceptable; values between 0.8 and 0.9 are excellent; and values >0.9 indicate outstanding discrimination (Swets, 1988).

For saltcedar, an estimated 591,394 1-km² grid cells in the western U.S. contain some suitable habitat, based on a binary map of the model created using the 10 percentile training presence threshold (0.52). (This does not mean that each 1-km² cell is completely suitable, so the estimated acreage covered by saltcedar would be considerably lower than that represented by the total acreage covered by 591,394 cells.) For saltcedar, the average training evaluation value was 0.93 and the average test evaluation value was 0.93 (Jarnevich *et al.*, 2011), indicating that the models were highly accurate. Using the same quarter quad dataset we described above as an independent test dataset, an evaluation value of 0.74 was calculated. Distance to water was always the most important predictor, and contributed an average of 44.2% to the model predictions. Suitability increased as distance to water decreased. Mean temperature of the warmest quarter and precipitation of the wettest month followed, with average contributions of 21.4% and 7.3% to the model predictions, respectively. The relationship with the warmest quarter is a logistic curve, where suitability is low at cooler temperatures, increases quickly at intermediate temperatures, and is greatest at high temperatures. Suitability is greatest with relatively lower precipitation in the wettest month.

Russian olive had 603 training locations and 258 test locations. Jarnevich and Reynolds (2010) developed two models, one with a coarse scale distance to water layer and the other with a fine scale one. The average values for the training and test evaluations were 0.94 and 0.91, respectively, for the coarse model and 0.92 and 0.89, respectively, for the fine model. Distance to water was the most important predictor in the coarse model, with an average contribution of 33.1% to the model. Habitat suitability decreased exponentially as distance to water increased. Suitability also tracked mean temperature of the wettest quarter (15.5%), precipitation seasonality (13.6%), and mean temperature of the warmest quarter (11.9%). In the fine scale model, distance to water was only the fifth most important predictor, indicating that Russian olive may be more sensitive to other variables when small water bodies are taken into account. Based on the coarse scale model (Figure 8b),

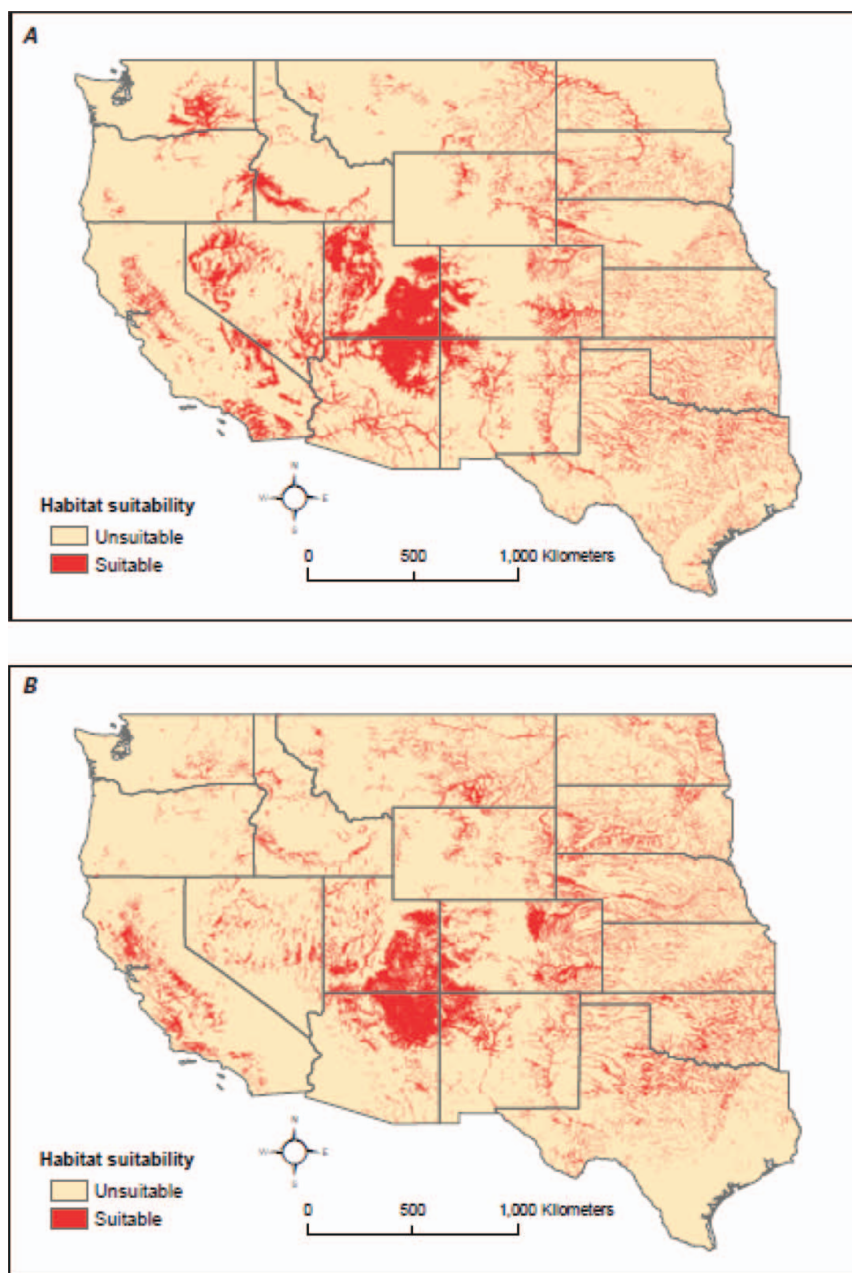


FIG. 8. Model results for (a) saltcedar and (b) Russian olive where habitat has been classified as suitable or unsuitable based on the 10th percentile training presence, meaning that the threshold to determine suitability correctly classifies 90% of the locations as suitable. A “suitable” location means that the grid cell (approximately 1 km²) in which the species is being predicted probably has some suitable habitat within it, not that the entire grid cell may be suitable (color figure available online).

601,920 1-km² grid cells in the western U.S. contain suitable habitat.

VII. CONCLUSIONS, DATA GAPS, AND FUTURE RESEARCH NEEDS

Saltcedar and Russian olive have been in the United States for over 100 years and are present in numerous locations. However, distribution maps based on simple presence-absence data

do not provide land managers with sufficient information to plan saltcedar control and riparian restoration projects. A functional assessment on a case-by-case basis is needed, in which positive and negative effects of these species on riparian ecosystems and hydrology are determined. This will require fine-scale, regional stream inventories that consider abundance levels of these species, niches within river reaches, and river characteristics that influence their abundance, such as flow regime, salinity, and degree of disturbance. The studies by Stromberg

et al. (2007b) and Merritt and Poff (2010) can serve as guides for developing a national-level inventory. At present, we do not have an adequate estimate of what percent of western riparian zones is resistant to dominance by either of these species, what percent is at risk and could benefit from intervention, and what percent has been altered to the point that saltcedar or Russian olive are likely to thrive even with intervention. However, we do have a better understanding of the constraints on saltcedar and Russian olive abundance and how they interact with native species compared to what we knew twenty years ago.

Similarly, numerical models of saltcedar and Russian olive [invasion] processes need to be improved. For both species, models reflect general habitat suitability for presence of the species, but not abundance. However, it is necessary to move on from models of habitat suitability to ones reflecting abundance and biomass to evaluate ecological and hydrological effects of these species. More research is needed to determine how models perform with biased datasets like those generally available for invasive species across large spatial extents. Most of these data are compiled from disparate efforts, each with unique sampling strategies. With presence-only data, we cannot differentiate poorly sampled areas from areas where the taxa are truly absent. Sampling incompleteness and uncertainty exacerbate the issues related to assessing sampling bias. Resultant models thus include unspecified uncertainty.

Problems also arise when algorithms treat the invasive species as a superior competitor that displaces native species from their established ecological niches, as this can result in overestimating the potential spread of saltcedar (Morissette *et al.*, 2006) and perhaps Russian olive, potentially causing needless concern among land managers and the public. Numerous studies (reviewed in Glenn and Nagler, 2005; Stromberg *et al.*, 2009) support the view that saltcedar has spread on western rivers primarily through a replacement process, where stress-tolerant species have moved into expanded niches that are no longer suitable for mesic, native, pioneer species. Future modeling efforts should incorporate such ecological findings.

Broad scale saltcedar removal could have profound effects on the distribution of native and introduced species and the habitat value of affected river systems (Hultine *et al.*, 2010), depending on the composition of vegetation that replaces saltcedar with or without restoration actions (Shafroth *et al.*, 2008). In recent years, leaf-eating beetles in the genus *Diorhabda* have been widely released in the western U.S. for the biological control of *Tamarix*, and they have spread rapidly in some watersheds (O'Meara *et al.*, 2010). Chemical control methods have also been applied on a large scale on some river systems (Hart *et al.*, 2005). The outcomes of control and restoration efforts will need to be incorporated into future distribution maps.

Furthermore, climate change could alter the distribution and abundance of saltcedar and Russian olive, via both direct effects on plants and indirect effects resulting from changes to

stream flow, biotic interactions and human activities. For example, direct effects of warming could shift species distributions northward and upstream (Parmesan, 2006). As discussed above, the dynamics of riparian vegetation are closely tied to stream flow and ground water regimes along rivers in the western U.S., both of which are already changing as a function of changing climate (Barnett *et al.*, 2008). Differential effects of climate change on native species versus saltcedar and Russian olive could alter competitive interactions and relative abundances. Again, these changes will need to be incorporated into future distribution maps as well as habitat suitability models.

By analogy to the triage system used in emergency medicine, we can postulate three broad classes of rivers where saltcedar (and perhaps Russian olive) occur. Free-flowing, perennial rivers typically have relatively low abundance of mature saltcedar because generally they do not compete well against mesic, native vegetation on these rivers (for example, perennial non-flow regulated streams [Stromberg *et al.*, 2007b; Merritt and Poff, 2010] and headwater streams in Sonora, Mexico [Scott *et al.*, 2009]). For these rivers, it is logical to conclude that saltcedar control is not needed unless complete eradication is the management objective. However, preserving the hydrologic regime of these rivers is important, as is preventing land use changes such as grazing, which can contribute to deterioration of the riparian zone and encourage the encroachment of saltcedar and Russian olive (Patten, 1998).

At the other end of the spectrum are highly regulated rivers where saltcedar and Russian olive have become dominant. These rivers have saline soils and aquifers that no longer provide niches for native species that are not drought and salinity tolerant (for example, the Lower Colorado River at Cibola National Wildlife Refuge; Nagler *et al.*, 2009). Logically, removing saltcedar from these rivers would not by itself improve the riparian zone. Similarly, removing Russian olive from highly flow-regulated rivers would not necessarily lead to the return of more desirable native species that depend on a natural flow regime to establish new cohorts, though far less is known about the dynamics of Russian olive.

The intermediate situation is characteristic of many river systems where the natural flow regime has been altered but not eliminated. These rivers often support mixed ecosystems of saltcedar, Russian olive, native cottonwood and willow trees, and native understory species. These rivers are perhaps the largest category in terms of acreage, yet we know the least about the invasion ecology of saltcedar and Russian olive on them.

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REFERENCES

- Akashah, O. Z., Neale, C. M. U., and Jayanthi, H. 2008. Detailed mapping of riparian vegetation in the middle Rio Grande River using high resolution multi-spectral airborne remote sensing. *J. Arid Envir.* **72**: 1734–1744.
- Akashi, Y. 1988. *Riparian Vegetation Dynamics Along the Bighorn River, Wyoming*. Ph.D. Dissertation, University of Wyoming, Laramie, WY.
- Anderson, B. 1998. The case for saltcedar. *Restor. Manag. Notes* **16**: 130–134.
- Barnett, T. P., Pierce, D. W., Hidalgo, H. G., Bonfils, C., Santer, B. D., Das, T., Bala, G., Wood, A. W., Nozawa, T., Mirin, A. A., Cayan, D. R., and Dettinger, M. D. 2008. Human-induced changes in the hydrology of the western United States. *Science* **319**: 1080–1083.
- Bay, R. F. and Sher, A. A. 2008. Success of active revegetation after *Tamarix* removal in riparian ecosystems of the southwestern United States: A quantitative assessment of past restoration projects. *Restor. Ecol.* **16**: 113–128.
- Bhattacharjee, J., Taylor, J. P. Smith, L. M., and Haukos, D. A. 2009. Seedling competition between native cottonwood and exotic saltcedar: implications for restoration. *Biol. Invasions* **11**: 1777–1787.
- Birkeland, G. H. 1996. Riparian vegetation and sandbar morphology along the lower Little Colorado River, Arizona. *Phys. Geog.* **17**: 534–553.
- Boudell, J. A. and Stromberg, J. C. 2008. Propagule banks: potential contribution to restoration of an impounded and dewatered riparian ecosystem. *Wetlands* **28**: 656–665.
- Bradshaw, G. L. 2006. Unpublished compilation of California *Tamarix* species locations. Colorado State University, Fort Collins, CO.
- Brand, L. A., White, G. C., and Noon, B. R. 2008. Factors influencing species richness and community composition of breeding birds in a desert riparian corridor. *Condor* **110**: 199–210.
- Brotherson, J. D. and Field, D. 1987. *Tamarix*: impacts of a successful weed. *Rangelands* **9**: 110–112.
- Busch, D. E. 1995. Effects of fire on southwestern riparian plant community structure. *Southwest. Nat.* **40**: 259–267.
- Busch, D. E. and Smith, S. D. 1995. Mechanisms associated with the decline of woody species in riparian ecosystems of the southwestern U.S. *Ecol. Monogr.* **65**: 347–370.
- Campbell, C. J. and Dick-Peddie, W. A. 1964. Comparison of phreatophyte communities on the Rio Grande in New Mexico. *Ecol.* **45**: 492–502.
- Carman, J. G. and Brotherson, J. D. 1982. Comparisons of sites infested and not infested with saltcedar (*Tamarix pentandra*) and Russian olive (*Elaeagnus angustifolia*). *Weed Sci.* **30**: 360–364.
- Christensen, E. M. 1963. Naturalization of Russian olive (*Elaeagnus angustifolia* L.) in Utah. *Am. Midl. Nat.* **70**: 133–137.
- Cleverly, J. R., Smith, S. D., Sala, A., and Devitt, D. A. 1997. Invasive capacity of *Tamarix ramosissima* in a Mojave Desert floodplain: the role of drought. *Oecologia* **111**: 12–18.
- Colorado Department of Transportation. 2002. *Colorado Department of Transportation geographic data*. Colorado Department of Transportation, Denver, CO. <http://www.dot.state.co.us/App.DTD.DataAccess/GeoData/index.cfm?fuseaction=GeoDataMain>, accessed June 15, 2009.
- Colorado Natural Heritage Program. 2008. *U.S. Air Force locations weed mapping data*. Colorado Natural Heritage Program, Fort Collins, CO.
- Colorado Weed Mapping. 2003. *2002 quarter quad survey*. Colorado Department of Agriculture, Denver, CO. <http://www.colorado.gov/cs/Satellite/Agriculture-Main/CDAG/1167928184069>, accessed June 15, 2009.
- Cornell, J. E., Gutierrez, M., Wait, D. A., and Rubio-Arbias, H. O. 2008. Ecological characterization of a riparian corridor along the Rio Conchos, Chihuahua, Mexico. *Southwest. Nat.* **53**: 96–100.
- Currier, P. J. 1982. The floodplain vegetation of the Platte River: phytosociology, forest development, and seedling establishment. Ph.D. dissertation, Iowa State University, Ames, IA.
- Dahm, C. N., Cleverly, J. R., Allred Coonrod, J. E. A., Thibault, J. R., McDonnell, D. E., and Gilroy, D. J. 2002. Evapotranspiration at the land/water interface in a semi-arid drainage basin. *Freshw. Biol.* **47**: 831–843.
- Davern, T. 2006. A predictive model: Tamarisk habitat in California and Colorado. M.S. thesis, Colorado State University, Fort Collins, CO.
- Di Tomaso, J. M. 1998. Impact, biology and ecology of saltcedar (*Tamarix* spp.) in the southwestern United States. *Weed Technol.* **12**: 326–336.
- Ellis, L. M. 2001. Short term responses of woody plants to fire in a Rio Grande riparian forest, Central New Mexico, U.S.A. *Biol. Conserv.* **97**: 159–170.
- Ellis, L. M., Crawford, C. S., and Molles, M. C. 1998. Comparison of litter dynamics in native and exotic riparian vegetation along the Middle Rio Grande of central New Mexico, U.S.A. *J. Arid Environ.* **38**: 283–296.
- Evangelista, P., Kumar, S., Stohlgren, T. J., Crall, A. W., and Newman, G. J. 2007. Modeling aboveground biomass of *Tamarix ramosissima* in the Arkansas River basin of southeastern Colorado, U.S.A. *West. N. Am. Nat.* **67**: 503–509.
- Evangelista, P. H., Kumar, S., Stohlgren, T. J., Jarnevich, C. S., Crall, A. W., Norman, J. B., and Barnett, D. T. 2008. Modelling invasion for a habitat generalist and a specialist plant species. *Divers. Distrib.* **14**: 808–817.
- Friedman, J. M., Auble, G. T., Shafroth, P. B., Scott, M. L., Merigliano, M. F., Preehling, M. D., and Griffin, E. K. 2005. Dominance of non-native riparian trees in western USA. *Biol. Invasions* **7**: 747–751.
- Friedman, J. M., Roelle, J. E., Gaskin, J. F., Pepper, A. E., and Manhart, J. R. 2008. Latitudinal variation in cold hardiness in introduced *Tamarix* and native *Populus*. *Evol. Appl.* **1**: 598–607.
- Gaskin, J. F. and Kazmer, D. J. 2006. Molecular phylogenetic investigation of U.S. invasive *Tamarix*. *Syst. Bot.* **28**: 86–95.
- Gaskin, J. F. and Schaal, B. A. 2002. Hybrid *Tamarix* widespread in U.S. invasion and undetected in native Asian range. *Proc. Natl. Acad. Sci.* **99**: 11256–11259.
- Gaskin, J. F. and Shafroth, P. B. 2005. Hybridization of *Tamarix ramosissima* and *T. chinensis* (saltcedars) with *T. aphylla* (athel) (family Tamaricaceae) in the southwestern U.S.A. determined from DNA sequence data. *Madroño* **52**: 1–10.
- Ge, S. K., Carruthers, R., Gong, P., and Herrera, H. 2006. Texture analysis for mapping *Tamarix parviflora* using aerial photographs along the Cache Creek, California. *Environ. Monit. Assess.* **114**: 65–83.
- Glenn, E. P. and Nagler, P. L. 2005. Comparative ecophysiology of *Tamarix ramosissima* and native trees in western U.S. riparian zones. *J. Arid Environ.* **61**: 419–446.
- Glenn, E., Tanner, R., Mendez, S., Kehret, T., Moore, D., Garcia, J., and Valdes, C. 1998. Growth rates, salt tolerance, and water use characteristics of native and invasive riparian plants from the delta of the Colorado River, Mexico. *J. Arid Environ.* **40**: 281–294.
- Graff, W. L. 1978. Fluvial adjustments to the spread of tamarisk in the Colorado Plateau region. *Bull. Geol. Soc. Am.* **89**: 1491–1501.
- Groeneveld, D. P. and Watson, R. P. 2008. Near-infrared discrimination of leafless saltcedar in wintertime with Landsat TM: *Int. J. Rem. Sens.* **29**: 3577–3588.
- Haber, E. 1999. *Invasive Exotic Plants of Canada Fact Sheet No. 14: Russian-olive*. National Botanical Services, Ottawa, Ontario, Canada.
- Hansen, N. E. 1901. *Ornamentals for South Dakota*. Bulletin 72, U.S. Experiment Stations, Brookings, SD.
- Harrison, J. and Matson, P. 2003. Patterns and controls of nitrous oxide emissions from waters draining a subtropical agricultural valley. *Global Biogeochem. Cycles* **17**: article no. 1080.
- Hart, C. R., White, L. D., McDonald, A., and Sheng, Z. P. 2005. Saltcedar control and water salvage on the Pecos River, Texas, 1999–2003. *J. Environ. Manage.* **75**: 399–409.

- Horton, J. L., Kolb, T. E., and Hart, S. C. 2001. Physiological response to groundwater depth varies among species and with river flow regulation. *Ecol. Appl.* **11**: 1046–1059.
- Hudgeons, J. L., Knutson, A. E., DeLoach, C. J., Heinz, K. M., McGinty, W. A., and Tracy, J. L. 2007. Establishment and success of *Diorhabda elongata* on invasive *Tamarix* in Texas. *Southwest. Entomol.* **32**: 157–168.
- Hughes, F. M. R. 1997. Floodplain biogeomorphology. *Prog. Phys. Geog.* **21**: 510–529.
- Hughes, F. M. R., Adams, W. M., Muller, E., Nilsson, C., Richards, K. S., Barsoum, N., Decamps, H., Foussadier, R., Girel, J., Guillo, H., Hayes, A., Johansson, M., Lambs, L., Pautau, G., Peiry, J. L., Perrow, M., Vautier, F., and Winfield, M. 2001. The importance of different scale processes for the restoration of floodplain woodlands. *Regul. Rivers: Res. Manage.* **17**: 325–345.
- Hultine, K. R., Belnap, J., van Riper, C., Ehleringer, J. R., Dennison, P. E., Lee, M. E., Nagler, P. L., Snyder, K. A., Uselman, S. M., and West, J. B. 2010. Tamarisk biocontrol in the western United States: Ecological and societal implications. *Front. Ecol. Environ.* **9**: 464–467.
- Jarnevich, C. S. and Reynolds, L. V. 2010. Challenges of predicting the potential distribution of a slow-spreading invader: a habitat suitability map for Russian olive (*Elaeagnus angustifolia*) in the western United States. *Biological Invasions* **13**: 153–163.
- Jarnevich, C. S., Evangelista, P., Stohlgren, T. J., and Morisette, J. 2011. An update to the national tamarisk map. *West. N. Am. Naturalist* **71**: 164–175.
- Jolly, I. D., Walker, G. R., and Thorburn, P. J. 1993. Salt accumulation in semi-arid floodplain soils with implications for forest health. *Journal of Hydrology* **150**: 589–614.
- Katz, G. L., Friedman, J. M., and Beatty, S. W. 2001. Effects of physical disturbance and granivory on establishment native and alien riparian trees in Colorado, U.S.A. *Divers. Distrib.* **7**: 1–14.
- Katz, G. L., Friedman, J. M., and Beatty, S. W. 2005. Delayed effects of flood control on a flood-dependent riparian forest. *Ecol. Appl.* **15**: 1019–1035.
- Katz, G. L. and Shafroth, P. B. 2003. Biology, ecology and management of *Elaeagnus angustifolia* L. (Russian olive) in western North America. *Wetlands* **23**: 763–777.
- Kefu, Z. and Harris, P. J. C. 1992. Effect of salt stress on nodulation and nitrogenase activity in *Elaeagnus angustifolia*. *Nitrogen Fixing Tree Research Reports* **10**: 165–166.
- Kelley, L. 2003. Otero County GIS weed mapping data. Otero County Weed District, Otero County, CO.
- Knopf, F. L. and Olson, T. E. 1984. Naturalization of Russian olive—Implications to Rocky Mountain wildlife. *Wildl. Soc. Bull.* **12**: 289–298.
- Lesica, P. and Miles, S. 1999. Russian olive invasion into cottonwood forests along a regulated river in north-central Montana. *Can. J. Bot.* **77**: 1077–1083.
- Lesica, P. and Miles, S. 2001. Natural history and invasion of Russian olive along eastern Montana rivers. *West. N. Am. Nat.* **61**: 1–10.
- Lite, S. J. and Stromberg, J. C. 2005. Surface water and ground-water thresholds for maintaining *Populus-Salix* forests, San Pedro River, Arizona. *Biol. Conserv.* **125**: 153–167.
- Lozon, J. D. and MacIsaac, H. J. 1997. Biological invasions: are they dependent on disturbance? *Environ. Rev.* **5**: 131–144.
- Mahoney, J. M. and Rood, S. B. 1998. Streamflow requirements for cottonwood seedling recruitment: an interactive model. *Wetlands* **18**: 634–645.
- Meinzer, O. E. 1927. Plants as indicators of ground water, U.S. Geological Survey Water Supply Paper 577. U.S. Geological Survey, Washington, DC.
- Merritt, D. M. and Poff, N. L. 2010. Dominance of a non-native riparian shrub along a gradient of flow alteration in rivers of the western U.S. *Ecol. Appl.* **20**: 135–153.
- Monk, R. W. and Wiebe, H. H. 1961. Salt tolerance and protoplasmic salt hardness of various woody and herbaceous ornamental plants. *Plant Physiol.* **36**: 478–482.
- Morisette, J. T., Jarnevich, C. S., Utah, A., Cai, W. J., Pedelty, J. A., Gentle, J. E., Stohlgren, T. J., and Schnase, J. L. 2006. A tamarisk habitat suitability map for the continental United States. *Front. Ecol. Environ.* **4**: 11–17.
- Mortenson, S. G., Weisberg, P. J., and Ralston, B. E. 2008. Do beavers promote the invasion of non-native *Tamarix* in the Grand Canyon riparian zone? *Wetlands* **28**: 666–675.
- Nagler, P. L., Glenn, E. P., Hinojosa-Huerta, O., Zamora-Arroyo, F., and Howard, K. 2007. Riparian vegetation dynamics and evapotranspiration for the riparian corridor in the delta of the Colorado River, Mexico: implications for conservation and management. *J. Environ. Manage.* **88**: 864–874.
- Nagler, P. L., Hinojosa-Huerta, O., Glenn, E. P., Garcia-Hernandez, J., Romo, R., Curtis, C., Huete, A. R., and Nelson, S. G. 2005. Regeneration of native trees in the presence of invasive saltcedar in the Colorado River delta, Mexico. *Conserv. Biol.* **19**: 1842–1852.
- Nagler, P. L., Morino, K., Didan, K., Erker, J., Osterberg, J., Hultine, K. R., and Glenn, E. P. 2009. Wide-area estimates of saltcedar (*Tamarix* spp.) evapotranspiration on the Lower Colorado River measured by heat balance and remote sensing methods. *Ecohydrol.* **2**: 18–33.
- National Park Service. 2003. Data and information: Data Clearinghouse, National Park Service. <http://www.nps.gov/gis/>, assessed June 15, 2009.
- Natural Resources Conservation Service. 2008. PLANTS profile, *Tamarix ramosissima* Ledeb., saltcedar, U.S. Department of Agriculture. <http://plants.usda.gov/java/profile?symbol=TARA>, assessed June 15, 2009.
- Neil, W. M. 1985. Tamarisk. *Fremontia* **12**: 22–23.
- Nelson, S. M. and Wydoski, R. 2008. Riparian butterfly (Papilionoidea and Hesperioidea) assemblages associated with *Tamarix*-dominated, native vegetation-dominated, and *Tamarix* removal sites along the Arkansas River, Colorado, U.S.A. *Restor. Ecol.* **16**: 168–179.
- North Dakota Department of Agriculture. 2003. *Tamarix mapping*, North Dakota. North Dakota Department of Agriculture, Bismark, ND.
- Olson, T. E. and Knopf, F. L. 1986. Agency subsidization of a rapidly spreading exotic. *Wildl. Soc. Bull.* **4**: 492–493.
- O'Meara, S., Larsen, D., and Owens, C. 2010. Methods to control saltcedar and Russian olive. In: *Saltcedar and Russian Olive Control Demonstration Act Science Assessment*, pp. 65–102. Shafroth, P. B., Brown, C. A., and Merritt, D. M., Eds., U.S. Geological Survey Scientific Investigations Report 2009-5247. USGS, Washington, D.C.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Syst.* **37**: 637–669.
- Patten, D. T. 1998. Riparian ecosystems of semi-arid North America: diversity and human impacts. *Wetlands* **18**: 498–512.
- Pearce, C. M. and Smith, D. G. 2001. Plains cottonwood's last stand: can it survive invasion of Russian olive onto the Milk River, Montana floodplain? *Environ. Manage.* **28**: 623–637.
- Pearce, C. M. and Smith, D. G. 2003. Saltcedar: distribution, abundance, and dispersal mechanisms, northern Montana, U.S.A. *Wetlands* **23**: 215–228.
- Pearce, C. M. and Smith, D. G. 2007. Invasive saltcedar (*Tamarix*): its spread from the American Southwest to the northern Great Plains. *Phys. Geog.* **28**: 507–530.
- Phillips, S. J., Anderson, R. P., and Schapire, R. E. 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* **190**: 231–259.
- Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Presegaard, K. L., Richter, B. D., and Stromberg, J. C. 1997. The natural flow regime: a paradigm for river conservation and restoration. *BioScience* **47**: 769–784.
- Read, R. A. 1958. *The Great Plains shelterbelt in 1954*, Publication No. 16. Great Plains Agricultural Council, University of Nebraska Experiment Station, Lincoln, NE.
- Reynolds, L. V. and Cooper, D. J. 2010. Environmental tolerance of an invasive riparian tree and its potential for continued spread in the southwestern US. *J. Veg. Sci.* **21**: 733–743.
- Ringold, P. L., Magee, T. K., and Peck, D. V. 2008. Twelve invasive plant taxa in U.S. western riparian ecosystems. *J. N. Am. Benthol. Soc.* **27**: 949–966.
- Robinson, T. 1965. *Introduction, spread and areal extent of saltcedar (Tamarix) in the western United States*. U.S. Geological Survey Professional Paper 491-A. U.S. Geological Survey, Reston, VA.

- Scott, M. L., Friedman, J. M., and Auble, G. T. 1996. Fluvial process and the establishment of bottomland trees. *Geomorph.* **14**: 327–339.
- Scott, M. L., Lines, G. C., and Auble, G. T. 2000. Channel incision and patterns of cottonwood stress and mortality along the Mojave River, California. *J. Arid Environ.* **44**: 399–414.
- Scott, M. L., Nagler, P. L., Glenn, E. P., Valdes-Casillas, C., Erker, J. A., Reynolds, E. W., Shafroth, P. B., Gomez-Limon, E., and Jones, C. L. 2009. Assessing the extent and diversity of riparian ecosystems in Sonora, Mexico. *Biodivers. Conserv.* **18**: 247–269.
- Scott, M. L., Shafroth, P. B., and Auble, G. T. 1999. Responses of riparian cottonwoods to alluvial water table declines. *Environ. Manage.* **23**: 347–358.
- Sengupta, D., Skiles, J. W., and Schmidt, C. L. 2005. *Tamarisk invasion in North-west Nevada*. Invasive Species Forecasting System Science Team Meeting, U.S. Geological Survey, 6–8 June 2005, Fort Collins, CO.
- Sexton, J. P., Sala, A., and Murray, K. 2006. Occurrence, persistence, and expansion of saltcedar (*Tamarix* spp.) populations in the Great Plains of Montana. *West. N. Am. Nat.* **66**: 1–11.
- Shafroth, P. B., Auble, G. T., and Scott, M. L. 1995. Germination and establishment of the native plains cottonwood (*Populus deltoides* Marshall subsp. *monilifera*) and the exotic Russian-olive (*Elaeagnus angustifolia* L.). *Conserv. Biol.* **9**: 1169–1175.
- Shafroth, P. B., Auble, G. T., Stromberg, J. C., and Patten, D. T. 1998. Establishment of woody riparian vegetation in relation to annual patterns of streamflow, Bill Williams River, Arizona. *Wetlands* **18**: 577–590.
- Shafroth, P. B., Beauchamp, V. B., Briggs, M. K., Lair, K., Scott, M. L., and Sher, A. A. 2008. Planning riparian restoration in the context of *Tamarix* control in western North America. *Restor. Ecol.* **16**: 97–112.
- Shafroth, P. B., Stromberg, J. C., and Patten, D. T. 2000. Woody riparian vegetation response to different alluvial water table regimes. *West. N. Am. Nat.* **60**: 66–76.
- Shafroth, P. B., Stromberg, J. C., and Patten, D. T. 2002. Riparian vegetation response to altered disturbance and stress regimes. *Ecol. Appl.* **12**: 107–123.
- Sher, A. A. and Marshall, D. L. 2003. Seedling competition between native *Populus deltoides* (Salicaceae) and exotic *Tamarix ramosissima* (Tamariceae) across water regimes and substrate types. *Am. J. Bot.* **90**: 413–432.
- Sher, A. A., Marshall, D. L., and Taylor, J. P. 2002. Establishment patterns of native *Populus* and *Salix* in the presence of invasive nonnative *Tamarix*. *Ecol. Appl.* **12**: 760–772.
- South Dakota Department of Agriculture. 2006. *Tamarisk weed mapping data, South Dakota*. South Dakota Department of Agriculture, Pierre, SD.
- Stoeckeler, J. H. 1946. Alkali tolerance of drought-hardy trees and shrubs in the seed and seedling stage. *Minnesota Acad. Sci.* **14**: 79–83.
- Stromberg, J. C. 1997. Growth and survivorship of Fremont cottonwood, Gooding willow, and salt cedar seedlings after large floods in central Arizona. *Great Basin Nat.* **57**: 198–208.
- Stromberg, J. C., Beauchamp, V. B., Dixon, M. D., Lite, S. J., and Paradzick, C. 2007a. Importance of low-flow and high-flow characteristics to restoration of riparian vegetation along rivers in arid south-western United States. *Freshw. Biol.* **52**: 651–679.
- Stromberg, J. C., Chew, M. K., Nagler, P. L., and Glenn, E. P. 2009. Changing perceptions of change: the role of scientists in *Tamarix* and river management. *Restor. Ecol.* **17**: 177–186.
- Stromberg, J. C., Lite, S. J., Marler, R., Paradzick, C., Shafroth, P. B., Shorrock, D., White, J. M., and White, M. S. 2007b. Altered stream-flow regimes and invasive plant species: the *Tamarix* case. *Global Ecol. Biogeogr.* **16**: 381–393.
- Stromberg, J. C., Tiller, R., and Richter, B. 1996. Effects of groundwater decline on riparian vegetation of semiarid regions: the San Pedro, Arizona. *Ecol. Appl.* **6**: 113–131.
- Swets, J. A. 1988. Measuring the accuracy of diagnostic systems. *Science* **240**: 1285–1293.
- Tamarisk Coalition. 2008. *Tamarisk Coalition Mapping Project*. Tamarisk Coalition, Grand Junction, CO.
- Tellman, B. 1997. Exotic pest plant introduction in the American southwest. *Desert Plants* **13**: 3–10.
- Thomas, K. and Guertin, P. 2007. Southwest non-native invasive plant database (SWEMP07): U.S. Geological Survey. Southwest Biological Science Center, Flagstaff, AZ.
- Uowolo, A., Binkley, D., and Adair, E. C. 2005. Plant diversity in riparian forests in northwest Colorado: effects of time and river regulation. *For. Ecol. Manage.* **218**: 107–114.
- U.S. Bureau of Land Management. 2006. *Utah noxious weeds: Salt Lake City, Utah*. Bureau of Land Management, Utah State Office, Salt Lake City, UT.
- van Riper, C., Paxton, K. L., O'Brien, C., Shafroth, P. B., and McGrath, L. J. 2008. Rethinking avian response to *Tamarix* on the lower Colorado River: a threshold hypothesis. *Restor. Ecol.* **16**: 155–167.
- Vieira, J. 2003. *Royal Gorge area weed mapping data*. U.S. Bureau of Land Management, Cañon City Field Office, Cañon City, CO.
- Walker, H. A. 2008. Floristics and phytogeography determine migrant landbird response to tamarisk (*Tamarix ramosissima*) invasion in riparian areas. *Auk* **125**: 520–531.
- Walker, L. R., Barnes, P. L., and Powell, E. A. 2006. *Tamarix aphylla*: a newly invasive tree in southern Nevada. *West. N. Am. Nat.* **66**: 191–201.
- Whitcraft, C. R., Talley, D. M., Crooks, J. A., Boland, J., and Gaskin, J. 2007. Invasion of tamarisk (*Tamarix* spp.) in a southern California salt marsh. *Biol. Invasions* **9**: 875–879.